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Earthworms

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Introduction

The productivity of an organism can best be estimated if it is abundant; easily sampled in all stages of its life cycle; and possesses characters from which its growth rate may readily be determined. Lumbricidae are often both irregularly and sparsely distributed; concealed at depths from which they cannot easily be removed; and seasonally inactive when they cannot be sampled by expellants. Their external sexual characters develop and regress irregularly and they lack other morphological characters from which their age might be determined; their growth rate is irregular, subject to environmental change and periodically negative. They are therefore difficult subjects for production studies.

Very few estimates of earthworm production have so far been attempted and these are necessarily approximate. The ensuing sections describe methods of sampling, estimation of biomass, procedures used in a study of production in *Lumbricus terrestris*, and some aspects of population metabolism studies.

Methods of sampling field populations

Of the numerous methods used to sample earthworm populations, none are equally suitable for all species and all habitats. They are of three types; those that employ irritant solutions or an electric current to expel the worms from the ground; those in which soil samples are taken from the field and the worms subsequently removed from them; and trapping methods. The choice of method must be based on the distribution and behaviour of the species concerned, the type of soil it occupies, and logistic considerations.

(1) Extraction methods

EXPELLENT METHODS

(a) *Potassium permangate solution method*

Evans and Guild (1947), in their pioneering studies on earthworm populations of agricultural soils in Britain, used potassium permanganate solution to expel worms from the soil, a method limited by the penetration of the solution and the variable response of earthworms to it. The method has been shown (Svendsen, 1955) to result for most species in considerable underestimates of population density and is not recommended.

(b) *Formaldehyde method*

The use of formaldehyde as an earthworm expellent was first described by Raw (1959) and has been found particularly useful for studies of *Lumbricus terrestris*. For species with a more horizontal and branching burrow system which the solution cannot easily penetrate it is less suitable and it is also unsuited for studies of aestivating species.

Concentration of solution. At Rothamsted, Raw tested solution strengths of 25 ml of 40% formalin in 1 gallon of water, approximately a 0·55% solution, and a quarter of this concentration, approximately 0·14%. The less concentrated solution expelled less than 50% of the number of worms expelled by the stronger solution in a population comprising mainly *Allolobophora chlorotica, A. caliginosa* and *A. rosea*. However, only seven pairs of quadrats were sampled and the difference may not have been significant.

Subsequent tests at Merlewood compared ten 0·5 m² quadrats each treated with four gallons (approximately 18 litres) of 0·165% formaldehyde solution with ten quadrats treated with 0·275% solution with the following results:

	0·165%	0·275%
Adult and large immature *L. terrestris*	76	75
Small immature *L. terrestris*	275	270
Other species	589	632
Total	940	977

The differences were clearly not significant.

Concentrations of 0·275% and 0·55% were similarly compared on 23 pairs of quadrats. The numbers of worms obtained were:

	0·275%	0·55%
Adult and large immature *L. terrestris*	420	429
Small immature *L. terrestris*	258	233
Other species	729	759
Total	1407	1421

These comparisons indicate that in the range 0·165% to 0·55% the concentration of solution is not critical. In subsequent studies at Merlewood, 0·275% solution (25 ml formalin in 2 gallons water) has been used.

Rate of application. The rate of application used by Raw (1959) was approximately 12 l/m² applied in two lots, the second about 20 minutes after the first. In a subsequent test on a woodland site at Merlewood, ten quadrats of 0·5 m² were treated with six applications each of 2 gallons (approximately 9 l, the capacity of a household bucket) of formaldehyde solution with 10 minute intervals between each application. Finally the top soil was removed and a further 2 gallons of solution was applied. The proportion of worms collected in each 10 minute interval is given in Table 1.

TABLE 1. The rate of expulsion of earthworms using successive applications of formaldehyde solution at 10 minute intervals.

	Number of worms (%) expelled between each application							
Application	1	2	3	4	5	6	7	Total Number Expelled
L. castaneus	79	19	1	0	1	0	1	85
A. chlorotica	74	18	3	2	1	1	0	407
L. terrestris	63	29	5	2	1	0	0	318
A. rosea	51	34	7	4	2	1	0	268
O. cyaneum	47	27	15	4	0	2	5	55
A. longa	41	41	10	0	3	3	3	39
A. caliginosa	40	37	16	5	1	1	0	141
All species	61	27	7		5			1313

It will be seen that the more active and/or surface-living species, e.g. *L. castaneus*, tend to emerge sooner than the deeper burrowing and/or less active species, e.g. *O. cyaneum*. However, taking all species together, 95% of the final catch had been expelled after three applications. As a better population estimate is likely to result from taking more samples than from striving

for extreme accuracy with fewer samples, the procedure recommended is to apply three lots of 2 gallons (9 litres) of 0·275% solution at 10 minute intervals to each quadrat of 0·5 m².

Correction for soil temperature and moisture. Both soil temperature and soil moisture content have been found to have an effect on the number of worms expelled by formaldehyde solution. In studies on *L. terrestris* in English woodland, the maximum response to formaldehyde occurred at about 10·6°C and the numbers expelled increased linearly with soil moisture content to 38% and decreased at 44%. The correction term found appropriate (Lakhani and Satchell, 1970) was:

$$\text{Estimated population} = \text{observed popln.} \times \exp.\{0{\cdot}0075\,(T - 10{\cdot}6)^2\} \times \exp.\{-0{\cdot}0214\,(M - 40)\}$$

where T = soil temperature at 10 cm in °C
and M = % soil moisture content.

The model on which this formula is based is discussed by Skellam (1967). It should be stressed that the values of the constants in the correction term apply only to *Lumbricus terrestris* on the sites studied.

Efficiency of the method. Raw (1959) compared a formalin treatment using 0·55% formaldehyde solution at the rate of approximately 24 l/m² (2 gallons per 4 sq ft) with hand sorting to a depth of 20 cm (8 in). The latter method produced fewer *L. terrestris* than the formalin treatment so the comparison throws no light on the efficiency of formalin as an expellent for this species. The following results were obtained for other species:

TABLE 2. Comparison of extraction by formalin and hand sorting from Raw (1959).

	Numbers per quadrat of 4 sq. ft (0·372 m²)			
	Arable soil		Under grass	
	Formalin	Hand sorting	Formalin	Hand sorting
L. castaneus	3·4	0·6	18·6	32·7
A. chlorotica	9·5	15·6	19·3	31·8
A. caliginosa	0·6	3·8	52·6	118·0
A. terrestris	0	0	3·1	7·7
A. rosea	2·4	7·5	11·3	55·2
O. cyaneum	4·8	6·3	3·0	8·2

At Merlewood, a one metre square quadrat and a 30 cm strip surrounding it, was treated with 0·275% formaldehyde solution in three applications each of 10 gallons (approximately 18 l/m²). The soil was then dug out to a depth

of 100 cm and sorted by hand. From the square metre, 52 *L. terrestris* and 193 worms of other species were expelled by the formaldehyde; 6 *L. terrestris* and 77 of other species were recovered by digging.

The correction factors for soil temperature and moisture content led to an estimate of 58 *L. terrestris* and 216 other species for the population of this quadrat. Three more *L. terrestris* were found by digging than were accounted for by the correction factors, suggesting that for this species, if no further worms were missed by the hand sorting, the population would have been correctly estimated. Other species would have been under-estimated by about one-fifth. A formal assessment of the efficiency of the formalin method awaits the development of a less laborious method for comparison than digging and hand sorting.

HAND SORTING

Hand sorting, though laborious, is a widely used sampling method which is also frequently used for assessing the efficiency of other methods. Its efficiency has been tested by Raw (1960) and Nelson and Satchell (1962).

Raw carried out tests on a wet hill grassland soil with a thick mat of vegetation in which worms were confined to the top of the profile. Samples were sorted by hand and the vegetation and mineral soil were then re-examined separately. The vegetation was teased out in water to which a few drops of formalin had been added to make the worms wriggle. The mineral fraction was worked through a 2 mm sieve to break up soil crumbs and was then immersed in magnesium sulphate solution on which the worms floated. Of the total worms found of all species, 52% of the number and 84% by weight were found by hand sorting. Only 38% of the total number and 57% of the total weight of a small species, *Eiseniella tetraedra*, were found by the hand sorting. From similar tests on a heavy arable soil, 59% of the total number and 90% of the total weight was found by the hand method.

Nelson and Satchell tested the method by sorting prepared samples into which known numbers of worms had been introduced. Samples of rough grassland were freed of live worms by freezing and specimens of various sizes and species, including pigmented and unpigmented forms, were introduced. Of 924 worms introduced, 93% (99% by weight) were found by hand sorting but only 80% of immature pigmented *Allolobophora chlorotica* and 74% of *Lumbricus castaneus* were recovered. In general the method seemed to give a satisfactory recovery of individuals weighing more than 0·2 g live weight but not of smaller worms. For studies aimed at producing life tables, hand sorting

would seem unlikely therefore to give a satisfactory recovery of the lowest age classes.

These tests were carried out with the operators knowing that their efficiency was being checked and may therefore have given an above-average recovery.

FLOTATION

The method used by Raw (1960) for extracting small species from soils unsuitable for hand sorting was based on an apparatus described by Salt and Hollick (1944). After preliminary washing, the organic material is floated off in magnesium sulphate solution in which the mineral soil sinks. The method has the advantage that it can be adapted to extract earthworm egg capsules and so enable all stages of the population to be estimated. Gerard (1967) states that in several tests this method extracted all the worms in the samples.

WET SIEVING

Washing soil with a jet of water through a series of sieves in the manner of Morris (1922) has been used by some authors, e.g. Krüger (1952), for collecting earthworms in studies concerned also with other faunal groups. There appears to be no published study of the efficiency of the method for extracting earthworms but its various disadvantages, e.g. damage to specimens and the long time and labour required to separate them from the residues, are listed by Ladell (1936). Raw (1960) found hand sorting much quicker than washing for both light and heavy soils. A method now under development (O'Connor, 1968) combines wet sieving with elution. The soil sample is broken up by water jets in the bottom of an inverted cone-shaped container, the dispersed sample flowing over an upper lip onto a submerged inclined sieve in another vessel. The soil passes through the sieve and the organic material moves downwards over its surface into a pipe leading to an elution unit. The flow of water through the pipe is such that the plant debris is carried up the elution column and the earthworms sink into a collecting chamber below it. The method has not yet been widely tested. The equipment is stated to process 4,000 cc of clay soil in one hour.

HEAT EXTRACTION

This method operates on the principle of the Baermann funnel (Baermann, 1917) and has been used for extracting small surface-living species from matted turf which would be difficult to sort by hand. The apparatus consisted of a plastic baby-bath, 55×45 cm, in which rested a wire gauze sieve 5 cm

from the bottom of the bath. A battery of fourteen 60 watt light bulbs held in a hardboard sheet rested on the rim of the bath on two battens so that when a soil sample was placed in the sieve, the light bulbs were suspended about 2 cm above it. The bath was filled with water to about half-way up the soil sample which was heated by the bulbs for three hours. The heating unit, sieve and contents were then removed, and the worms were collected from the water immediately. The soil samples used in this apparatus were generally 20 × 20 cm × 10 cm deep.

The following results were obtained from a comparison of methods on a *Deschampsia flexuosa* site in an acid oak wood in which 90% of the earthworm population was *Bimastos eiseni*. Of 20 0·5 m^2 quadrats, ten were treated with formaldehyde solution (2 applications 0·275% + 1 application 0·55%, soil temperature 10°C), as previously described. The soil and litter to a depth of 10 cm was removed from the remaining quadrats, that from three being sorted by hand while the remaining seven were heat extracted. The times taken to hand sort the three samples were $7\frac{3}{4}$, $9\frac{1}{2}$ and $12\frac{1}{2}$ hours. The mean numbers of worms per sample were: formalin 3·4; hand sorting 15; heat extraction 26.

TRAPPING

For very low population densities no satisfactory sampling methods have as yet been developed but baiting and trapping techniques have been found useful in comparative studies. Svendsen (1957) studied a *Calluna* moor from which fifty 20 cm^3 soil cores yielded only one specimen of *Dendrobaena octaedra*. By examining at intervals 66 pieces of dung placed at the intersections of a 5 × 10 m grid he was able to analyse seasonal activity. The volume of the piece of dung was found to be important, pieces of 600, 300 and 150 ml yielding mean numbers of 58, 32, and 18 worms respectively over a period of 14 days. Boyd (1957) used prepared dung pats of 800 ml but these were disturbed by birds.

An alternative method in which the sorting may be carried out indoors is to prepare traps with a layer of ground dung over a layer of peat in a shallow earthenware plant pot. The traps are sunk to ground level and collected after 14 days for inspection in the laboratory. Thirty such traps laid out in acid oak woodland in Roudsea Wood National Nature Reserve yielded 84 *Bimastos eiseni* from an area of 120 m^2, an average of 0·7/m^2. Twenty soil cores from the same site treated by the heat extraction method gave an estimate of the *B. eiseni* population of 23·75 ± 1·01/m^2. Although trapping methods are

unlikely to yield accurate population estimates they can form a useful means of studying activity patterns where population densities are low.

(2) Determination of size and number of samples

Having decided on the appropriate extraction method, the investigator must then determine the size and number of sampling units required for population estimates of known accuracy.

Sampling unit area

A number of workers have followed Wilcke (1955) in selecting a sample unit area of 50 × 50 cm and a depth of 40 or 50 cm. Zicsi (1958) compared samples of this size with units of 25 × 25, 50 × 100 and 100 × 100 cm. He found that the number of worms per m^2 recovered by hand sorting decreased with increasing size of sample, indicating an increase in tediousness and hence of inefficiency in sorting the larger samples. In an arable soil the average number of worms estimated per m^2 from 50 units of each size were 25 × 25 84·5; 50 × 50 77·7; 50 × 100 62·8; 100 × 100 62·6. A tool for taking soil samples of 25 × 25 cm (1/16 m^2) to a depth of 20 cm is described by Zicsi for use in soils which are not too stony. Svendsen (1955) used a steel scoop of semicircular cross-section to cut cores 283 sq. cm (1/35 m^2) in area and 20 cm deep. The minimum sample area which will prove satisfactory will depend largely on the density of the populations to be sampled.

Number of sampling units

The number of samples which needs to be taken to ensure a population estimate of specified accuracy will depend on their size and the density and degree of aggregation of the population. This must be ascertained in the particular case by trial sampling but the following data from some typical temperate European sites (Table 3) indicate the sampling variance likely to be encountered. It will be found that a sampling error of less than 10% of the mean cannot generally be obtained without an excessive cost in sampling effort.

Biomass estimation

(1) Loss in weight during preservation

The British Museum (Anon., 1932) recommends preservation of earthworms in 70—90% alcohol after a preliminary fixing in 10% formaldehyde, but

TABLE 3. Numbers of samples required for estimating population means of given sampling error

	Numbers/0·5 m²									
1. A population of *L. terrestris* sampled by the formalin method	25	28	25	35	15	24	15	18	17	22
	Numbers/sq. ft									
2. A population of *A. caliginosa* sampled by an electrical method	7·7	1·0	5·4	6·0	4·2	7·0	3·8	11·8	3·7	7·0
	Numbers/sq. yd in a quadrat 8×8 yd									
3. A population of *L. castaneus* sampled by the permanganate method.	3, 2, 2, 4, 7, 7, 3, 3, 2, 1, 0, 0, 0, 1, 1, 5, 9, 1, 3, 3, 0, 0, 7, 0, 5, 4, 9, 9, 8, 8, 0, 2, 0, 0, 4, 12, 14, 6, 1, 1, 5, 3, 5, 0, 2, 7, 2, 0, 1, 14, 7, 4, 6, 4, 4, 2, 1, 6, 2, 0, 2, 6, 3, 1, 0.									

Number of samples required to give a sampling error of the mean equal to	5%	10%	20% of the mean
L. terrestris population	32	8	2
A. caliginosa population	103	26	7
L. castaneus population	358	89	23

ecologists more frequently use formalin as a preservative at concentrations of 4–10%. In both preservatives loss of weight occurs: at Merlewood, *L. terrestris* preserved in 70% alcohol were found to have lost 10% of their fresh weight in four days and Raw (1962) stated that the weight of worms preserved in 5% formalin is 25% less than the fresh weight. It is important to note that this weight loss varies with time as indicated by the following data from 50 *L. terrestris* preserved for 4 months.

TABLE 4. Loss in weight (%) of *L. terrestris* preserved in 4% formalin.

After	24 hours	7 days	1 month	4 months
Loss in weight	6·4	10·1	12·9	17·9

The worms used for these observations ranged in size from 1 g to 4 g. No relationship between size and the proportion of weight lost was detected. There is some evidence that greater weight losses may occur in some other species. This factor must therefore be taken into account when biomass estimates are to be based on samples of preserved worms.

(2) Conversion of fresh weight to dry weight

The analysis of the size class distribution of an earthworm population requires large numbers of worms to be weighed individually. If they are first

collected into preservative this must be removed from the surface of the worm before weighing. The common practice of rolling the specimen on a cloth or filter paper is difficult to standardize and can be a source of serious error. It can be eliminated by determining the live weight/dry weight ratio and applying this to individual worm weights obtained from subsequent samples which have been collected into preservative, oven dried at 105°C and weighed from a dessicator. In studies where a life table can be determined solely from samples collected from the field it may be possible to work entirely on a dry weight basis but where the growth rate has to be computed in part from culture data the use of live weights is unavoidable. Regression analysis of the data from 44 specimens of *L. terrestris* which were weighed live, preserved for 4 days in 4% formalin, dried at 105% and reweighed, gave the relation:

1 g dry weight ≙ 5·5 g live weight

From a larger body of data, Lakhani and Satchell (1970) obtained the relation

1 g dry weight ≙ 6.37 g live weight

In preparing estimates of the biomass of earthworm populations the weight of the gut contents should not be overlooked. A sample of 10 *L. terrestris* taken from the field and dissected had gut contents weighing 20% of the fresh weight of the whole worms but this value varied with the size of the worm. In a further sample of 30 worms selected to include a wide size range, the dry weight of the gut contents was on average 29% of the dry weight of the whole worm and ranged from 26% in worms of about 0·5 g live weight to 41% in worms of 7 g live weight. The regression of percentage weight of gut content on body size was significant at the 1% probability level. This result may have arisen from loss of gut material during dissection of the smaller worms or it may indicate that the gut is larger in proportion to the body in larger worms or that the larger worms ingest a higher proportion of mineral matter in their diet than the smaller worms. Bouché (1966a) has described a method of washing out the gut contents of large lumbricids employing a catheter and syringe and (1966b) a technique for measuring biovolume as an alternative to biomass.

Estimation of relative productivity

Relative productivity is defined as the ratio of the annual turnover of biomass to the average prevailing biomass. A first attempt to estimate it for two populations of *L. terrestris* has been made using the formaldehyde sampling technique and biometrical methods devised by J.G. Skellam and M.D.

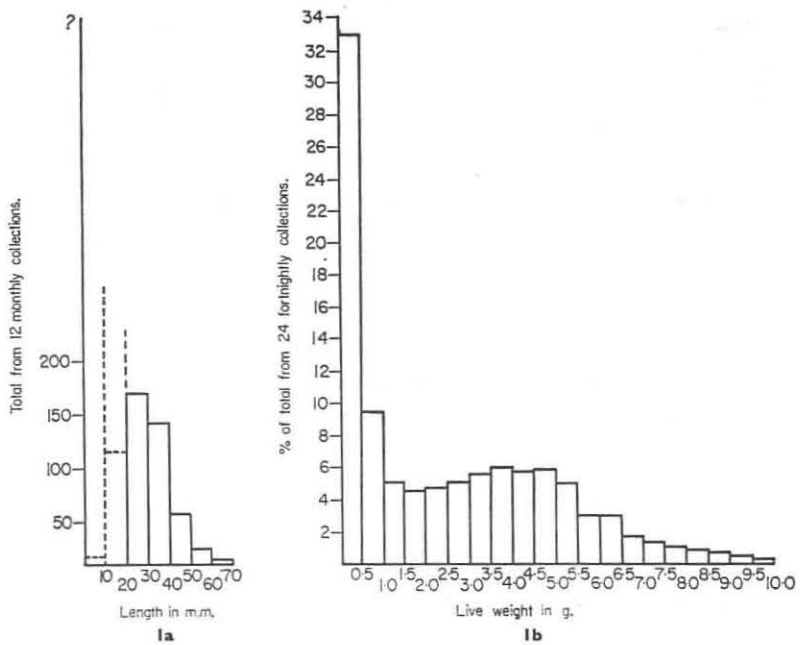

Figure 1a. Size class distribution of a population of *Eisenia rosea* (from Murchie, 1958).

Figure 1b. Size class distribution of a population of *Lumbricus terrestris* (Satchell, unpublished).

Mountford. The estimates are based on the size class structure of the populations, their growth rates and their mortality and survivorship curves. The methods described below are largely drawn from this work an account of which has been published elsewhere (Lakhani and Satchell, 1970).

(1) Size class structure

The size class structure of a population of *Allolobophora rosea* (calculated from Murchie, 1958) is shown in Figure 1a. Although the size classes are expressed in units of length which are less suitable for productivity studies than units of weight, the histogram illustrates the size class distribution typical of a species in which few individuals survive long after reaching the average maximum size. The data were obtained by hand sorting a soil sample of standard volume each month and expressing the numbers in each size group as a percentage of the total collected in the year. The smallest size

class is under-represented because of the limitations of the hand sorting method. The histogram would otherwise have shown a continuously descending curve.

Figure 1b shows the size class structure of a population of *Lumbricus terrestris* sampled by the formaldehyde method (data from Lakhani and Satchell, in prep.). It illustrates the size class distribution of a species in which many individuals live on after the average maximum weight is attained. The histogram shows a hump at about 4·25 g which is interpreted as an accumulation of mature worms at about the average upper size limit for the species in the prevailing field conditions.

(2) Construction of growth curves

The construction of growth curves is straightforward for species in which the population overwinters as cocoons and the young worms hatch simultaneously and mature and die off with no overlap of generations. In these circumstances, provided that the population of newly hatched worms can be estimated adequately, the rate of growth in the field can be calculated directly from successive size class frequencies. Such straightforward cases are unfortunately rare, the more usual situation being that many sizes of worms are present in the population concurrently.

In *Lumbricus terrestris* the cocoons hatch mainly in the spring. This generates a peak in the size class distribution which can be followed for several months by determining the modal values of the weights of the worms collected at each sampling. Taking these values as the average weight of the worms on each sampling date, the growth curve can be constructed for about the first year. Thereafter the mode is obscured by the wide variation in growth rate of individual worms.

It may be possible in some studies to continue the growth curve by consideration not of the increase in average size with time, but of the average time taken to reach a given weight. If the growth curve is in a sharply ascending phase the modal value of the time class distribution at a certain weight will be more sharply defined than that of the weight class distribution at a certain time.

Beyond the point where these methods are applicable, the growth curve may be extended by use of culture data. The culture method used by the author for *L. terrestris* was to put newly hatched worms collected from the study population individually into nylon bags of worm free soil and leaf litter taken from the study site. These were buried on the site so that the litter

was level with the soil surface. The worms were weighed initially and re-weighed and re-provisioned at monthly intervals. Because of the great variability in growth rate of individual worms a large number of specimens should be set up in culture; sixty were used in the work referred to.

This method keeps the worms at field moisture and temperature and mortality was much lower than when glass or earthenware containers were used. Food was doubtless more readily available than under field conditions and the culture worms grew faster and attained a greater maximum size than worms in the field population.

Before culture data can be used for constructing growth curves, it must be established that the general pattern of growth in culture is the same as that in the field. It may be possible to establish this for the beginning of the growth curve by comparing the growth in culture with that obtained from analysis of the size class distribution in the field. For the latter part of the growth curve this is likely to remain an unverifiable assumption. However, the sensitivity of the estimate of relative productivity to hypothetical departures of the culture growth curve from the field growth curve can be tested by appropriate models.

If it is established or assumed that the pattern of growth in culture is not materially different from that in the field, the next step is to adjust the rate of growth in culture to that in the field. This may be done by reference to

(1) the weight attained in the field at the last point where this can be deduced from the size class distribution
(2) the asymptotic weight attained in the field
(3) the weight attained in the culture at the time corresponding to weight (1)
(4) the asymptotic weight attained in the cultures.

Suppose (a) it had proved possible to construct a growth curve for the field population by analysing the movement of peaks in the size class distribution for 9 months and that the mean weight of the worms at 9 months was 1 g;
(b) the asymptotic weight in the field was 4 g (cf. Fig. 1b);
(c) the mean weight of the culture worms at 9 months was 2 g;
(d) the asymptotic weight of the culture worms was 8 g (cf. Fig. 2),

then the factor relating growth in the field to growth in the cultures would be:

$$(4-1)/(8-2)=0{\cdot}5$$

The growth curve from 9 months onwards could then be constructed by taking the weight increase in the field to be 0·5 times the weight increase in the cultures in the corresponding time interval.

Figure 2. Growth increment and mortality (- - - -) of *L. terrestris* reared outdoors.

(3) Construction of survivorship curves

For species in which most of the worms hatch at about the same time, survivorship curves may be constructed on the basis of the subsequent decline in the numbers of young worms. A size class histogram for such a species in the months after hatching will show an abundance of worms of very low weight followed by an absence of worms of slightly higher weight and then, in species with overlapping generations, the presence of worms of all higher weight classes. Assuming that the worms of higher weight are survivors of previous generations, data of this type can be conveniently tabulated in the following way:

	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.
1969 generation	250	224	199	146	130	188	110	97	92	80	63	46
Previous generations	200	192	211	186	179	159	165	195	167	175	180	189

In such a case the April worms might represent 250 of 1 month old and 200 of 13+25+37+ . . . months old, the May worms 224 of 2 months old and 192 of 14+26+38+ . . . months old, *et seq.*

The appropriate model for the survivorship curve will have to be constructed to suit the particular case and will be suggested by the shape of the survivorship curve of the worms in culture. It is likely to decline steeply at first when the worms have recently emerged from the cocoons, then to flatten out and finally to decline again as the worms become senile (cf. Fig. 2). This pattern can be described mathematically by the survivorship function

$$S(t) = \frac{1 - a\,t^k}{1 + bt}$$

where S = number surviving to age T
and t = time

a, the maximum age, and b and k are the parameters to be estimated. These may be determined by the method of maximum likelihood from the numbers counted at different times of the year and the age structure of the population.

(4) Relative productivity

The production by one generation of worms is the sum of the products of the numbers dying at all ages and their weights at death. The production per month is the sum of the product of the weight at death and the proportion of the generation dying in that month, i.e. the prevailing death rate. The relative productivity per month is the production per month expressed as a fraction of the prevailing biomass (standing crop).

Expressed mathematically, relative productivity on a monthly basis may be estimated by

$$\frac{\int_0^\infty \mu\,(a)\,S\,(a)\,W\,(a)\,d\,a}{\int_0^\infty S\,(a)\,W\,(a)\,d\,a}$$

where (a) = the death rate at age a,
and $S\,(a)$ = proportion of earthworms surviving to age a, both obtained from the survivorship curve,
and $W\,(a)$ = average weight of the earthworms at age a obtained from the growth curve.

Population metabolism

The preceding section indicates procedures which may be found useful in estimating one component in the energy budget equation: Amount of food ingested = amount of tissue produced + amount lost in respiration + amount excreted.

(1) Ingestion

The amount of food ingested by earthworms depends upon (1) the rates of movement of material through the gut under different conditions, (2) the duration of these conditions. For species defaecating on the soil surface, estimates have been based on regular collections of worm casts (Evans, 1948) but for other species, authors (Barley, 1959; Satchell, 1967) have been able to suggest only approximate quantities based on estimates of the number of days in the year in which the worms might have been feeding. The rate of soil ingestion is known to depend on whether or not the worm is burrowing and to vary with environmental factors and the worm's physiological condition. A comprehensive analysis of these factors leading to a critical assessment of annual food intake has not yet been attempted.

The rate of movement of soil through the gut of *L. terrestris* has been studied by Parle (1963) using ^{32}P as H_3PO_4 as a tracer. Worms were kept singly in pots of soil containing pellets of labelled dung and peat and were dissected at intervals after the pellets had been taken. The results suggested that under the conditions of the experiment, food passed through the gut in about 20 hours. A similar result has been obtained (Satchell, unpublished) from worms kept initially in a light coloured subsoil then transferred to a dark topsoil.

(2) Excretion

From arguments based on laboratory estimates of nitrogen excretion rates of *L. terrestris* (Needham, 1957) and the seasonal pattern of soil temperature and biomass of a field population, Satchell (1963) suggested that the annual output of excreted nitrogen for this population might be of the order of 3·3 g/m². If we assume that this was in the form of 64% mucus, 16% urea and 20% ammonia as recorded by Needham for feeding worms, and that the calorific value of mucus is about 4·0 kcals/g and of urea is 2·5 kcals/g, the energy content of the non-faecal excreta produced by this population would appear to be of the order of 9 kcals/m²/year. The tissue production of this

population is perhaps about 100 g live weight/m²/year. Assuming that (a) 1 g dry weight = 5·5 g live weight; (b) 30% of the dry weight is gut content; and (c) the calorific content of earthworm tissue is 4·42 kcals/g (French, Liscinsky and Miller, 1957), the calorific content of the tissue produced may be about 56 kcals/m²/year. Thus the energy content of the excreted metabolites may form a substantial component in the energy equation.

The measurement of the production of these metabolites has so far been attempted only under standard laboratory conditions and it is difficult to assess how the production of, for example, mucus in laboratory glassware relates to its production in undisturbed conditions in the soil. An alternative technique is being studied in which worms are 'labelled' by feeding them on organic matter containing N_{15}, transferring them to natural soil and measuring the rate of disappearance of the isotope from the tissues by analysis of specimens taken at successive time intervals.

(3) Respiration

A number of respiratory studies on lumbricids are currently in progress and it is premature to suggest which methods are most appropriate for the group. In three of the most recent studies the methods used were (1) a modified Lindgren method (Gromadska, 1962); (2) Warburg respirometry (Byzova, 1965); and (3) infra-red gas analysis (Bolton, 1967). As with population metabolism studies of other groups, the following factors are known to affect earthworm respiration:

Size. The respiratory rate per unit weight is higher for small specimens of a given species than for large specimens. This is well illustrated by Gromadska's (1962) data for *L. castaneus* and Krüger's (1952) data for *E. foetida* and is consistent with Konopacki's (1907), Davis and Slater's (1928) and Raffy's (1930) observations on *L. terrestris*. Byzova (1965) has shown that the dependence of respiratory rate on body size is marked for surface-active species (*Dendrobaena octaedra, Eiseniella tetraedra, L. castaneus, L. terrestris, O. lacteum*) but is almost lacking in subsurface-living unpigmented species (*A. caliginosa, A. rosea*).

Activity. Most workers in this field have sought to measure the respiratory rate of resting animals but Raffy (1930) gives some indication of the variation in metabolic rate with diurnal activity in *L. terrestris*. In observations continued for 48 hours, the maximum oxygen consumption rate was 13% higher than the minimum rate. Exposure to light, however, may double the respiratory rate (Davis and Slater, 1928). There are to date no published studies

describing the activity pattern of field populations on which a realistic estimate of population metabolism could be based.

Ambient temperature. The respiration rate rises with increasing temperature. In poikilotherms generally, the magnitude of the temperature effect, described by the Arrhenius constant μ, has a value of 11,500 calories for a wide variety of respiratory processes. From experiments done at temperatures ranging from 9—27°C, a μ value of 11,040 calories has been found for *L. terrestris* (Pomerat and Zarrow, 1936) so the relationship between temperature and respiratory rate in earthworms appears to be similar to that reported for other poikilothermous animals. Acclimatization has been demonstrated in the tropical earthworm *Megascolex mauritii* in which the rate of oxygen consumption at 20°C was shown to be greater for winter animals than for summer animals by about one-third in large specimens to four times in small specimens (Saroja, 1961).

Soil atmosphere. Johnson (1942) and Byzova (1966) have demonstrated the dependence of respiratory rate on oxygen tension in experiments with mixtures of oxygen and nitrogen. Byzova found that soil dwelling species with a low respiratory rate are relatively insensitive to a drop in oxygen tension while surface-active species are most sensitive. The oxygen consumed in 10% O_2 expressed as a percentage of the consumption at atmospheric concentration was approximately, for *D. octaedra* 63%, *E. foetida* 70%, *L. terrestris* 93% and *A. caliginosa* and *A. rosea* 100%.

It is generally believed that carbon dioxide concentrations in the soil do not affect respiration greatly. *Eisenia foetida* shows no behavioural response to concentrations up to 25% by volume (Shiraishi, 1954), and Stephenson (1930) states that the presence of CO_2 up to a proportion of 50% has only a slight and reversible effect on earthworms. Extreme limits of CO_2 concentration in soils quoted by Russell (1950) range between 0·01 and 11·5%.

The respiratory data from various authors and the population estimates for English Lake District woodlands referred to earlier suggest that the annual oxygen consumption of these populations of *L. terrestris* may be of the order of 23 l/m² and the energy of respiration about 110 kcal/m² per annum. The energy of tissue production appears to be about half this amount and the energy excreted as metabolites perhaps one-twelfth.

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